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# Sex differences and seasonal variation in habitat choice in a high density population of Waterbuck, *Kobus ellipsiprymnus* (Bovidae)

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## Abstract

Habitat use of waterbuck *(Kobus ellipsiprymnus)* was recorded during road transect counts in Lake Nakuru National Park, Kenya. Waterbuck were encountered significantly more often in open (riverine) forest and open grassland than expected from a random distribution through the available habitat types. There were significant differences in habitat use by different age and sex classes, with the lowest percent overlap (85 %) between adult females and young males. Seasonal differences in habitat use correlated with rainfall: with increasing rainfall waterbuck moved into open grassland, during periods of low rainfall waterbuck moved into open shrub.

## Introduction

Waterbuck are antelopes the size of red deer; they occur throughout Africa south of the Sahara (Dorst and Dandelot 1970; Haltenorth and Diller 1977). The two subspecies *Kobus ellipsiprymnus ellipsiprymnus* and *K. e. defassa* interbreed in areas of geographical overlap, e.g. Nairobi National Park, Kenya (Backhaus 1958; Kiley-Worthington 1965). Next to impala (cf. Leuthold 1977; Jarman 1979), waterbuck probably is the antelope species studied most intensively (references in Spinage 1982 and Tomlinson 1980b, 1981; Melton 1983).

The population at Lake Nakuru National Park, Kenya, belongs to the subspecies *K. e. defassa*. With an average of 30 waterbuck per km$^2$, regionally up to 100/km$^2$, Lake Nakuru NP has by far the highest density recorded for waterbuck (Kutilek 1974; Wirtz 1978).

The high population density can be expected to have effects on the social behaviour of the species. In three earlier publications (Wirtz 1981, 1982, 1983a) the social behaviour was described. In the following we present data on habitat utilization and on how it varies seasonally and between age and sex classes.

## Study area

Lake Nakuru is a shallow alkaline lake at an altitude of 1760 m in the eastern Rift valley, about 130 km northwest of Nairobi, Kenya. Lake Nakuru has become famous as "the lake of a million flamingoes"; up to 1.4 mill. flamingoes have been recorded there (Vareschi 1978). To protect the spectacular avifauna of the lake and its shorelines, the area was declared a bird sanctuary and later a National Park.

A vegetation map of the park is given by Wirtz (1982, fig. 1). Open grassland is dominated by *Cynodon dactylon, Themeda triandra, Chloris gayana,* and species of *Andropogon* and *Hyparrhenia;* near the lake shore the soda-resistant *Sporobolus spicatus* is abundant. Open and dense shrub is formed by patches of *Tarchonantus camphoratus, Lantana trifolia,* and *Pluchea ovalis.* Open and dense forestes are formed by *Acacia xanthophloea, Olea africana* and other *Acacia* species (all species identifications based on Curry-Lindahl [1971] and Kagumaho Kakuyo [1980]). Both study years

were exceptionally wet years compared to long term means (KUTILEK 1975); see fig. 2 for monthly rainfall values.

The density and biomass of the larger mammals has been described by KUTILEK (1974) and WIRTZ (1978, 1983b). A checklist including the rarer species was given by WIRTZ (1979) and the group size frequencies of the eight most common antelope species was described by WIRTZ and LÖRSCHER (1983). Waterbuck are the dominant larger mammal species in terms of numbers and in terms of biomass.

## Material and methods

Field work lasted for 25 months, from November 1977 to December 1979. At the beginning of each month, all roads and tracks of the park were followed with a Landrover. Whenever an individual or a group of waterbuck was seen, the sex and age class of all members of the group and the habitat were noted on a dictaphone. A definition of the age and sex classes used (calves, subadult females, adult females, juvenile males, young males, adult males) is given in WIRTZ (1982). Any waterbuck which could not be assigned to one of the age and sex classes (e.g. because it was partially hidden by the vegetation) was called "unidentified". Counts were made from 7.00 am to 9.30 am and not during heavy rainfall; it took five to seven days to cover the whole park.

The total length of the strip counted in this way was 114 km. Strip width differed according to vegetation. During three of the counts, the distance from the road to each group of waterbuck was estimated, which gives the average sight distance in the different types of habitat. To determine the relative areas of the different habitat types, a separate count was made: While driving the Landrover at a constant speed of 20 mph, the type of habitat to the left and to the right was noted every 2 seconds. The proportion of each habitat along the counting strip multiplied with the average sight distance gives a measurement of the relative sizes of the areas: Table 1.

*Table 1.* **Relative size of the different types of habitat along the counted transect**

| habitat type | proportion along the counting strip (% of records) | average sighting distance (m) | relative size of counting area (% of total) |
|---|---|---|---|
| open grass | 33.39 | 107.89 | 53.46 |
| dense shrub | 12.67 | 22.83 | 4.29 |
| open shrub | 31.86 | 57.67 | 27.27 |
| dense forest | 5.03 | 30.00 | 2.24 |
| open forest | 14.15 | 45.21 | 9.50 |
| others | 2.90 | 75.17 | 3.24 |

For most of the variables described in the "Results' section, we have used the data for a "representative year" from August 1978 to July 1979 (n = 3017 groups, cumulative number of animals recorded 17064).

## Results

### Population composition and an estimate of the variance produced by the counting method

Table 2 shows the average population composition for the year August 1978 to July 1979. About a third of the population consisted of adult females. The sex ratio of adult and subadult animals was not significantly different from 1:1 (50.7 % ♂♂:49.3 % ♀♀;

*Table 2.* **Population composition (annual mean)**

| | adult males | young males | juvenile males | adult females | subadult females | calves | unidentified |
|---|---|---|---|---|---|---|---|
| n seen in the 12 counts | 3253 | 3068 | 987 | 5353 | 1830 | 1055 | 1518 |
| % (mean of the monthly percentages) | 19.1 | 18.0 | 5.8 | 31.4 | 10.7 | 6.2 | 8.8 |

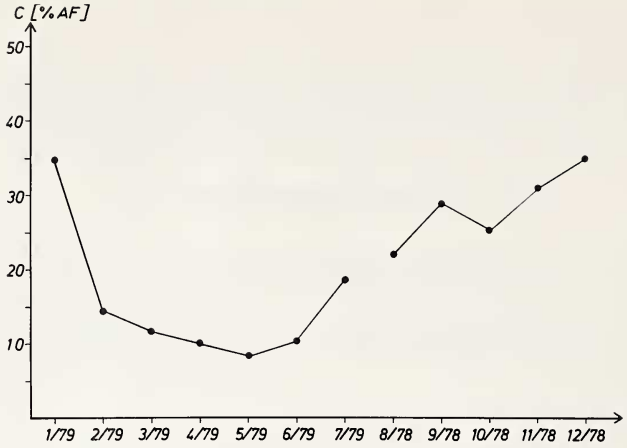


*Fig. 1.* Monthly variation in the number of calves per hundred adult females

$p > 0.2$, t-test). The sex ratio of adult animals was 1:1.6 (♂♂ : ♀♀). The percentage of calves in the population varied from 2.9 (June) to 9.7 (December); fig. 1 shows the numbers of calves per hundred adult females during the course of the year.

How accurate are the monthly counts? A second count was begun immediately after the first one in June 1979 and in September 1979. Table 3 compares the results. Even though

*Table 3.* **Comparison of the results of two consecutive counts**
(percent of each age class in the total)

| | adult males | young males | juvenile males | adult females | subadult females | calves | unidentified | n animals |
|---|---|---|---|---|---|---|---|---|
| June 79–A | 19.4 | 18.6 | 6.5 | 35.0 | 10.9 | 2.9 | 6.7 | 1576 |
| June 79–B | 19.3 | 21.8 | 7.5 | 31.5 | 11.0 | 4.1 | 4.9 | 1282 |
| Sept. 79–A | 16.0 | 23.4 | 5.5 | 34.6 | 8.2 | 5.9 | 6.4 | 1571 |
| Sept. 79–B | 16.2 | 17.6 | 4.1 | 38.8 | 9.5 | 6.8 | 7.1 | 1629 |

the absolute number of animals counted during the first and second count can differ by as much as 300, the percentage of each age class in the total was very similar in the two counts made during the same month. The counting procedure apparently gives well-reproducible results.

## Habitat utilization

### *General pattern*

Table 4 compares the relative frequencies of habitat types availabe (from table 1) and the proportions of waterbuck counted in them during the 12 months. Most of the habitat covered during the counts consisted of open grassland and most waterbuck were seen in open grassland. However, waterbuck were not evenly distributed throughout the available habitat types: a larger proportion of waterbuck was seen in open grassland than expected for an even distribution ($p < 0.001$, chi-square test).

*Table 4.* **Habitat availability and the proportion of waterbuck seen in the different types of habitat**

| | open grass | open shrub | dense shrub | open forest | dense forest | others |
|---|---|---|---|---|---|---|
| proportion of animals counted (n=17064) | 57.2 | 21.4 | 4.5 | 15.5 | 0.7 | 1.0 |
| relative size of area | 53.5 | 27.3 | 4.3 | 9.5 | 2.2 | 3.2 |

### *Age and sex specific trends*

There were sex differences and age differences in the distribution of waterbuck: Table 5.

The distribution of each age class differs with $p < 0.001$ from an even distribution through the available habitat types (chi-square test). A considerably larger proportion of adult males was seen in open grassland than expected for an even distribution (compare

*Table 5.* **Percentage of different age classes and sexes in the different types of habitat (annual mean)**

| | adult males | young males | juvenile males | adult females | subadult females | calves | unidentified |
|---|---|---|---|---|---|---|---|
| open grass | 64.56 | 59.21 | 50.99 | 50.55 | 51.78 | 56.88 | 69.40 |
| open shrub | 19.27 | 26.38 | 29.74 | 20.11 | 20.15 | 17.68 | 19.94 |
| dense shrub | 2.54 | 2.56 | 5.05 | 5.92 | 5.11 | 4.02 | 3.88 |
| open forest | 12.50 | 11.03 | 13.18 | 20.58 | 20.45 | 19.57 | 6.10 |
| dense forest | 0.49 | 0.27 | 0.49 | 1.32 | 0.73 | 0.96 | 0.27 |
| others | 0.65 | 0.56 | 0.56 | 1.52 | 1.79 | 0.89 | 0.41 |
| n animals | 3253 | 3068 | 987 | 5353 | 1830 | 1055 | 1518 |

with lower part of table 4). In contrast, adult females were seen in open grassland less often than expected and in open forest much more often than expected. The difference in distribution pattern of adult males and adult females is significant with $p < 0.001$ (chi-square test).

A comparison of the different age classes shows how the sex-specific distribution pattern becomes more pronounced from calf to adult animal. Calves (which remain hidden during the first two to four weeks of their life; Spinage 1982) were seen in open shrub and open forest more often than expected for an even distribution. The distribution of subadult females has shifted to an even stronger preponderance in open shrub and open forest (comparison with calves: $0.10 p < p < 0.05$, chi-square test). Compared to subadult females, adult females were found more often in dense shrub and approximately equally often in open shrub and open forest ($0.2 < p < 0.1$). The distribution patterns of calves, juvenile males, young males, and adult males differ significantly ($p < 0.001$) in each comparison: with increasing age the males change from open forest, dense shrub and open shrub to open grassland.

A numerical expression of similarity (or difference) in habitat utilization is given in the percent overlap. For each class, the proportion using the different habitat types is calculated (i.e. table 5); then the lower of the two percentages of the classes that are compared is summed over all habitat types to give the percent overlap. Table 6 shows the results: the highest overlap in habitat use (98.5 %) was between adult females and subadult females, the lowest overlap (85.1 %) was between adult females and young males. The average overlap in habitat use of classes belonging to the same sex (92.5 %) is higher than the average overlap of classes belonging to a different sex (87.5 %).

*Table 6.* **Percent overlap in habitat use**

| | adult males | young males | juvenile males | adult females | subadult females | calves |
|---|---|---|---|---|---|---|
| adult males | 100 | | | | | |
| young males | 92.9 | 100 | | | | |
| juvenile males | 86.8 | 91.8 | 100 | | | |
| adult females | 86.0 | 85.1 | 89.9 | 100 | | |
| subadult females | 87.2 | 86.3 | 90.4 | 98.5 | 100 | |
| calves | 90.7 | 89.0 | 86.9 | 93.7 | 94.7 | 100 |

*Seasonal variation*

From month to month, there could be large differences in the proportion of waterbuck counted in the same habitat. Fig. 2 illustrates this by showing the percentage of adult females counted in open grass and in open shrub from August 1978 to July 1979; between

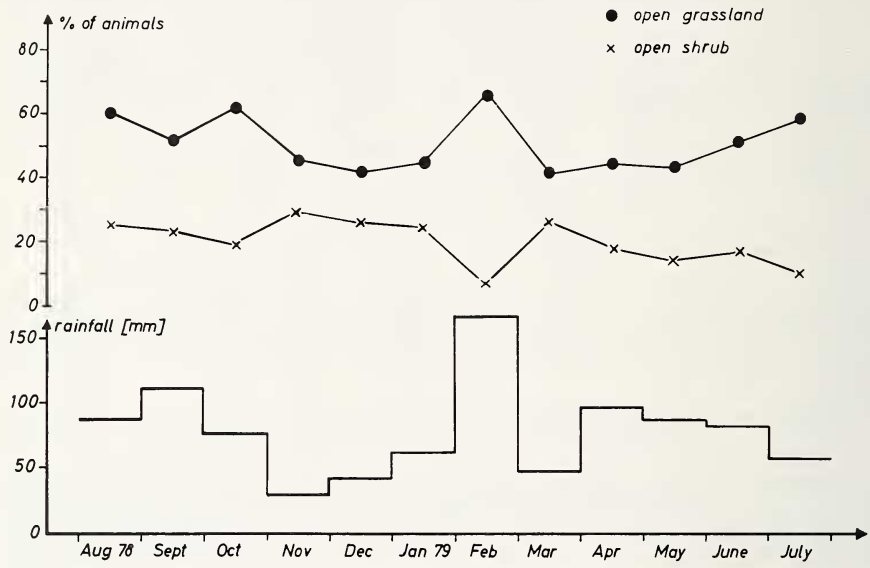


*Fig. 2.* Monthly variation in the percentage of adult females in open grassland and in open shrub and monthly variation in rainfall

7 % and 30 % of the adult females were counted in open shrub and between 41 % and 66 % in open grassland. For a total of 15 months, there were data on rainfall and on habitat use (habitat was unfortunately not recorded during all of the road strip counts). Rainfall and habitat use correlate in the following way: there was a negative correlation between the amount of rain falling in a month and the percentage of animals counted in open shrub ($p < 0.05$ for all animals and for adult females alone, SPEARMAN rank test); there was a positive correlation between the amount of rain falling and the percentage of animals counted in open grassland ($0.1 > p > 0.05$ for all animals and $p < 0.05$ for adult females alone, SPEARMAN rank test); there was no discernible correlation between the amount of rain falling in a month and the percentage of animals counted in dense shrub, dense forest,

and open forest. With decreasing rainfall the proportion of waterbuck counted in open grass decreased and the proportion of waterbuck counted in open shrub increased. Note that the second statement is not a necessary consequence of the first statement but a separate finding: animals leaving open grass areas could have dispersed into several other types of habitat. With increasing rainfall waterbuck moved from open shrub to open grassland, with decreasing rainfall waterbuck moved from open grassland to open shrub.

There is no definite calving season in Nakuru waterbuck; newborn calves were seen throughout the year. The percentage of calves counted did, however, increase sharply during July to September (fig. 1). We tested whether adult females, in any month, changed habitat use in a different direction than did adult males. While there were differences in the degree of change in habitat use, the directions of shift of adult females and of adult males resembled each other and corresponded to the pattern shown in fig. 2.

## Discussion

Waterbuck depend on permanent access to water; they almost completely lack the ability to reduce water loss in response to a shortage of water (Taylor et al. 1969) and they tend to occur close to areas where water is readily available (e.g. van Lavieren and Esser 1979; Spinage 1982; Sinclair 1985). In Nakuru National Park nearly all areas covered during the counts, including "open grassland", were within three kilometres' distance to water and most of the "open forest" was forest along rivers draining into Lake Nakuru. Due to the exceptional amounts of rain during the study period, the waterholes were always full.

Waterbuck groups are open groups; they continuously change their size and composition. From a group in, for instance, open grassland some animals may wander off into adjacent forest, while others from nearby open shrub may join those in grassland. Individuals apparently make an independent choice and the number of animals (instead of the number of groups) in a certain habitat has therefore been used as a measure of habitat utilization.

Statements on habitat use of waterbuck in the literature are sometimes based on the proportion of animals seen in different types of habitat but without relating these proportions to the relative areas available (e.g. Spinage 1982). In the most extensive study of antelope-habitat relationships, Hirst (1975) showed that the waterbuck of the Transvaal lowveld (South Africa) occured in riverine gallery forest more often than expected for an even distribution through available habitat types. No preference for open grassland was indicated in Hirst's study. Caution must be used in the interpretation of such differences between study areas because the nature of the habitat described with the same name may differ in subtle ways which are nevertheless important to the animals. Whereas most of the Nakuru grassland was close to water, the grassland in Hirst's study area may not have been. Jarman (1972) and Sinclair (1985) also found a preference of waterbuck for riverine forest and for grassland in the Zambezi valley and in Masai Mara National Park.

Different visibility of the different age classes may have affected the counts and the apparent age differences could be an artefact. However, only for calves is this likely to be true: in dense habitat calves are more likely to be overlooked than larger animals and this may have resulted in an overestimate of the proportion of calves in open habitat.

We assume that the pattern of habitat use shown by the animals is adaptive, i.e. that animals using certain habitat types at a given time have a higher chance of survival and/or reproductive success. Food, predation and climate are the factors most likely to be of importance (but see Peek et al. 1976 for an example of the influence of parasites). Differences in habitat utilization between age and sex classes can be due to differences in their requirements and/or to different action of external variables. Seasonal differences can be due to changes in requirements and/or changes in external variables.